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THE NEUROMUSCULAR STRUCTURE OF SEA-ANEMONES

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Sea-anemones are more or less cylindrical animals that are usually attached to some rock or other fixed object by one end, the pedal disc, and carry on the opposite end or oral disc a single opening, the mouth. This opening, surrounded by tentacles, leads through a short oesophagus into the single internal cavity of the animal, the digestive cavity, and serves not only for the admission of food but also for the discharge of waste. The portion of the animal that connects the pedal disc with the oral disc is the column wall. This wall like that of the oral and of the pedal disc, consists of an outer layer of cells, the ectoderm, and an inner layer next the digestive cavity, the entoderm. These two layers are separated by an intermediate layer of secreted material containing cells, the supporting lamella. The entoderm of the column wall is thrown into vertical folds, the mesenteries, which project from the inner face of this wall into the digestive cavity. In the deeper parts of both ectoderm and entoderm are sheets of muscle fibers by whose contraction the whole animal can retract greatly. This form of retraction and the reverse process of expansion are among the commonest activities of the sea-anemone. These operations involve not only the muscle layers just mentioned, but also a primitive nervous mechanism associated with them.

The muscle layers in sea-anemones are not the undifferentiated sheets implied in many of the earlier accounts of the structure of these animals, but fall into fairly well defined separate muscles. In the species of sea-anemone that we studied most fully, *Metridium marginatum* of the New England shore, there are thirteen differentiated muscles or groups of muscles. The longitudinal muscle of the tentacles is found on the ectodermic surface of these organs. The circular muscle of the tentacles covers their entodermic faces. The radial muscle of the oral disc spreads from the region of the mouth over the ectodermic surface of the disc to its outer edge. The circular muscle of the oral disc covers the entodermic face of this disc. The circular muscle of the oesophagus surrounds this organ on its entodermic side. The circular muscle of the pedal disc is a broad, circular sheet on the entodermic face of this part of the animal. The basilar muscles are radial muscles attached to the mesenteries where these join the pedal disc. The longitudinal muscles of the mesenteries extend in the mesenteries from the pedal disc to the oral disc. The transverse muscles of the mesenteries are at right an-

gles to the longitudinals and extend from the outer wall of the sea-anemone to the inner free edge of the mesentery or to the oesophagus when the mesentery unites with that organ. The parietal muscles of the mesenteries are longitudinal strands in the mesenteries at the region of attachment of these organs to the column wall. The circular muscle of the column covers the entodermic face of the column wall. The sphincter is a specialized band in the circular muscle of the column which it surrounds at a level close to the oral disc. The longitudinal muscles of the acontia are extremely tenuous muscles in these filamentous organs.

The nervous system of sea-anemones consists of sense cells said to be in the entoderm as well as in the ectoderm whose deep ends form a nervous network in close proximity to the muscles. This network includes in its meshes ganglion cells. In 1879 the Hertwigs described a concentration of nervous material in the oral disc of sea-anemones and believed this to be the beginnings of a central nervous organ. Gröselly claimed that the nervous centralization is in the oesophagus. Many recent workers, however, have declared the nervous system to be diffuse and not centralized at all.

According to most investigators the ectodermic nervous network connects with the entodermic one only in the region of the mouth where these two layers are confluent being separated in other places by the supporting lamella. Havet, however, in 1901 claimed that nervous tissue could be traced through the supporting lamella thus connecting ectoderm and entoderm directly. We have found evidence of this both histological and physiological. By special staining methods we have confirmed Havet's statement that the supporting lamella contains nervous elements and by experiment we have shown that these elements connect the ectoderm *directly* with the longitudinal muscles of the mesenteries (entoderm), that is, without passing through the mouth region. If a small area on the ectoderm of the column wall is stimulated mechanically or chemically, the sea-anemone will retract the oral disc through the action of the longitudinal muscles of the mesenteries. If this area is partially isolated by making a circular incision around it and completely through the column wall so that it is attached to the animal only by the deep-lying mesenteries, the longitudinal muscles in these organs will regularly contract on stimulating its ectodermic face. Thus there must be direct nervous connections between the ectoderm of the column wall and the longitudinal muscles of the mesenteries, and this connection appears to consist of a relatively complex but diffuse nervous network.

A second type of neuromuscular structure is seen in the outer layer of

the tentacles of *Metridium*. Here ectodermic sense cells connect directly with the underlying longitudinal muscle fibers and thus these fibers are brought into action without the intervention of so extensive a network as in the former instance.

What seems to be a third type of neuromuscular mechanism is seen in the circular muscle of the column of *Metridium*. If the exterior of the column of this animal is stimulated mechanically, retraction generally follows. If the spot stimulated is anesthetized by allowing a few crystals of magnesium sulphate to dissolve on it and it is then stimulated, general retraction does not result but in the course of a minute or so a band formed by a local contraction in the circular muscle of the column appears and gradually spreads around the column. This band of contraction then slowly disappears. The reaction is apparently due to the direct stimulation of the circular muscle of the column, a muscle which from other grounds is known to be open to indirect stimulation probably through the nervous network.

A fourth type of muscular activity is seen in the longitudinal muscles of the acontia. If these filamentous organs are detached from a *Mertidium*, they will live hours in ordinary sea-water moving about in tortuous lines by means of their cilia. If such free acontia are stimulated mechanically, they slowly tangle themselves up and afterwards slowly untangle. If now they are subjected to what would be thorough anesthetization with chloretone and are again mechanically stimulated, they tangle themselves up as before. Apparently their muscle is entirely independent of nerves and under ordinary conditions is brought into action by direct stimulation.

These four types of muscle action are of phylogenetic significance. The last mentioned, that of the longitudinal muscle of the acontium, is the most primitive and resembles the type found in sponges in that it is slow in action and not under nervous control. The next in advancing complexity is the circular muscle of the column partly independent and partly under nervous influence. The third, the longitudinal system of the tentacle, is a well defined union of sense cells and muscle fibers and is relatively quick in action. Finally the most complex type is the sense cell, complex nervous network, and muscle fiber as first described, a quickly responding, most highly differentiated example. These four types show that the neuromuscular mechanism of sea anemones is by no means so simple and uniform as was originally supposed but embraces a variety of structural conditions which serve different purposes and probably represent evolutionary steps.

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